VOL. XIII. NO. 10.—BOTANICAL GAZETTE.—OCT., 1888.

Development of cork-wings on certain trees. I.

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The name cork-wing has been applied to ridges of corky substance extending lengthwise along the young stems of certain trees and woody shrubs. One very prominent example is that of Liquidambar styraciflua, a tree which in the southern states attains a large size, the young branches of which are ridged with this cork formation, so that the tree, when standing leafless, has the appearance of being supplied with a set of troughs to conduct off the water.

This peculiar habit of growth is exhibited by several other species of trees, which, however, differ less in appearance from the ordinary bark-producing tree. Such are certain maples, oaks, elms and a few others. The peculiarity of the Liquidambar tree is that the wings of the lateral branches project mainly from the upper side, thus giving the tree in winter the curious appearance before mentioned. It was with reference to this one-sided growth, together with the large amount of material seen to be expended in what seems a useless appendage, that a brief study of the manner of formation of these wings was undertaken. This led to a similar study of some of the other trees referred to above. In the literature of cork and its development, this peculiarity is mentioned as of sufficient importance to admit of its receiving a particular name, but, so far as I have been able to learn, no special examination has been made of the so-called cork wings as distinguished from other forms of corky projections from the surface of dicotyledonous and coniferous growths. Dr. Carl Sanio, in his work on cork,[1] remarks, with true scientific candor, "It is extremely difficult to study the development of cork wings." Sanio's ability as an investigator and the amount and value of his contributions to botanical science are too well known to require proof here, and as this remark occurs in connection with what he says of the Liquidambar tree, it may be well to explain at the outset that the following results are not given as representing an ex-

[1] Pringsheim's Jahrbücher, 1860. Vol. II. Page 39.

haustive study even of the few species examined, but rather as an introduction to an intended wider and more detailed investigation.

In the whole range of vegetable anatomy there is, perhaps, no other subject about which so much has been written, which still remains so obscurely treated in the ordinary text-book as that of cork formation in general, and more especially of that peculiar process which leads to the formation of bark. One reason for this is, without doubt, the lack of agreement among different authors in the use of the terms referring to the outer growths of woody stems of dicotyledons and gymnosperms. For example, several text-books, written in English, differ in the definition of the term bark, which, though acknowledged to be a general, rather than scientific term, still deserves to be used in a manner to make clear what part of the stem is meant. Another very probable reason is, the difficulty of the subject itself and the fact that each successive author, in writing upon it, introduces new terms and partially modifies the old. Owing to these facts, a summary of the terms used, with their definitions, together with a brief history of the subject, may be allowed before entering upon a description of the work done.

As to its history, it is, perhaps, unnecessary to state that cork was one of the first objects of microscopical investigation, as this was purely accidental. Robert Hooke, about the middle of the seventeenth century, invented an improvement on the compound microscope of that time, and in order to show the importance of his invention, used pieces of cork among other objects. H. von Mohl was the first to publish a description of cork in an article entitled, Untersuchungen über die Entwickelung des Korkes, etc.[2]. In this he showed that the bark owes its origin to the development of cork-lamellæ inside the rind.[3] Rudolf Müller[4] followed him, but his work was limited to the relation of the cork to the other tissues of the rind of deciduous trees. Later, Hanstein,[5] Schacht[6] and Schleiden[7] made various studies in this field. After

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[2] Verm. Schriften, p. 212.

[3] *Rind* here in the general sense of German "Rinde," *i. e.*, all that part of the stem outside the cambium ring. Primary rind, those cells of the fundamental tissue of the stem between the epidermis and the ring of vascular bundles. Secondary rind, all the phloem tissue, both of the original vascular bundles and whatever secondary growth may be added from the cambium layer.

[4] Breslau Dissertation.

[5] Untersuchungen über den Bau und die Entwickelung der Baumrinde.

[6] Der Baum.

[7] Grundzüge der Wissenschaftl. Botanik. 3d edition. Page 283.

them came Sanio, who says that the previous investigations have reference mainly to the relation between cork and the other rind cells, and that, while they make clear the meaning of this tissue in the household of cork-building plants, the history of its development, the law governing the succession of cell growth, etc., has not yet received attention. Schleiden had made the mistake of supposing the development to originate in all cases from the epidermal cells. Von Mohl and Hanstein attributed it to the first layer of primary rind cells. Sanio now made a more thorough study of it in reference to this point, and showed that there is no uniformity as to the place of origin of the cork tissue, but that it begins, in some cases, in the epidermal tissue, in others, in the first layer of primary rind cells, or in the second or third layer, and finally it may originate more or less irregularly, deeper in the rind tissues. The layer of cells which take on this activity, beginning to grow and divide, thus forming new tissue, was first named *cork cambium*. Nägeli named it *phellogen*. Sanio showed that from this layer the cells of the cork tissue were cut off toward the circumference; the same phellogen layer could also cut off cells toward the center of the stem, growth proceeding both in a centripetal and centrifugal direction. There was, however, this difference, the cells cut off toward the circumference were more or less corky in nature, while those developed on the opposite side of the phellogen layer became parenchymatic tissue and might contain chlorophyll.

In 1877 von Höhnel[8] took up the subject again with special reference to the chemistry of the tissue, and gave as a reason for his investigations that, up to that time, the question, "What is the suberin of authors?" had not been answered; that there were two principal views on the subject, the one, that suberin is nothing more than a physical modification of cellulose; the other, that it is itself a substance forming an integral part of the wall whose foundation is cellulose. The latter view is fully sustained by his researches. He says suberin is just as distinctly a substance as cellulose or lignin. Farther than this, he shows how it is distributed in the wall and how it may be detected. By these tests he proves that much of the tissue heretofore considered cork consists largely of lignin, that these tissues alternate with each other, the lignin being produced early in the season, the suberin later.

It will be impossible to make clear what follows without

[8]Sitz. Berichte der Wiener Akad. d. w. Nov. 1877. LXXVI. I. p. 587.

an explanation of the technical use of terms as generally agreed upon by different authors on this subject, taking De Bary as authority wherever differences exist. Sanio named the cells cut off from the phellogen toward the center of the stem *phelloderm*, those cut off toward the circumference *phellem;* von Mohl made a distinction between the plate-formed cells, that is, those of short radial diameter, and the longer ones, naming the former cork, the latter periderm cells; this distinction being considered unscientific, inasmuch as both are developed alternately from the same layer, De Bary,[9] who wished to retain the term periderm, determined to refer to this word all that tissue originating from the phellogen layer. So that, as the terms are now used, periderm consists of two kinds of tissue, that developed from the phellogen, found on the outside of this layer, which is named phellem, and that formed on the inside of this layer, named phelloderm. According to von Höhnel, the phellem consists, or may consist, of two kinds of tissues—true cork cells, whose walls are suberized, and ligneous cells, whose walls are mainly wood. These latter are called phelloid, the former cork, and this without reference to the form of the cells, the substance of the cell wall being the ground of distinction. According to the plan of origin of the phellogen cells, there are two kinds of periderm, called superficial and deep-seated, sometimes, also, primary and secondary, as the superficial, when present, always precedes the deep-seated in order of time. De Bary makes this division, describes the superficial periderm and then says, "the position of the internal is not determinate in a sense generally applicable to all cases," and that this is owing to the number of transition forms between it and the superficial. He does not give the exact position of the phellogen layer of the internal periderm. Joseph Moeller,[10] in his Anatomie der Baumrinde, gives four classes of superficial periderm, considered with reference to the exact position of the phellogen layer. These, he says, may be reduced to three, when genetically considered. Of these three, the first is when the phellogen layer is the epidermis; the second, when it is situated in the primary rind; the third, when in the phloem of the vascular bundles. This last, he says, may be considered a transition form between the superficial and the deep-seated. For the latter, it must be inferred its place is in the phloem of the secondary growth,

[9]Comparative Anat. of Phanerogams and Ferns (Eng. trans.), pp. 114 and 544.
[10]Anatomie der Baumrinden. Vergleichende Studien von Dr. Joseph Moeller. Berlin, 1882.

or the phloem produced by the cambium ring after it is completed around the stem.

Difficult as it is to harmonize the different ways of describing the processes of periderm formation, as given by various writers, nearly all agree in the main features of that by which bark is produced, viz: bark is the product of the internal or deep-seated periderm, and it consists of all that portion of rind-tissue outside of this periderm, which tissue, cut off from nourishment by the corky layers of periderm, dies and is eventually thrown off. This is the *Borke* of the Germans and the *ecorce crevassée* of the French.[11] One form of internal periderm originates from phellogen cells extending in a nearly continuous layer around the stem; this gives rise to the so-called ring-bark, examples of which are Vitis and Clematis. Another form of internal periderm arises deeper in the rind of certain stems on which there is already a superficial periderm. The phellogen cells of this form, instead of extending in one layer around the whole circumference, arise in such a manner that, as De Bary expresses it, "they abut on the outermost layer of periderm for the time being," referring here to the repeated formation of internal periderm; the cork thus formed cuts off bark in the form of scales. The favorite example of this is the Platanus. Hence the two kinds, ring- and scale-bark. Now, accepting the definition of bark given by De Bary[12], we must exclude all those trees from the list of bark-bearing ones which do not have, at some period, one of the two forms of internal periderm. He quotes this definition, however, from von Mohl, and does not himself adhere strictly to it, as on a page or two previous he gives an instance of phellogen arising in the second or third subepidermal layer and cutting off a *small bark*. This, according to both De Bary and Moeller, must be considered as a superficial periderm, and the latter adheres more consistently to the definition of bark, inasmuch as he gives only 83 genera of bark-producing trees among the 392 specimens which he examined, and he expressly states that these 83 kinds possessed internal or secondary periderms.

Now, according to De Bary's explanation of superficial periderm, which differs from Moeller's only in its lack of definiteness, it is with this kind of periderm alone that our subject has to do. In connection with this, is one point sel-

[11] Traite de Botanique par J. Sachs. Traduit de l'allemand sur la 3d edition et annote par Ph. von Tieghem. 1874.

[12] Comp. Anat. p. 551.

dom noticed in text-books, and that is, that the superficial periderm also gives rise to two kinds of coverings, which De Bary names suberous crusts and suberous integuments (kork-krusten und kork häute). These two forms owe their origin to the difference in the manner of development of the cork or corky layers. Here De Bary classifies, apparently without reference to form of cell or nature of wall, meaning by cork the phellem, or all outside the phellogen layer. Where this develops with nearly equal rapidity around the whole circumference, it forms the suberous integument; where, owing to some cause, the development is irregular, certain portions of the phellogen producing faster than others, suberous crusts are formed, and it is in this category that he puts the cork-winged trees, together with all those having deep, irregular furrows and ridges along their surface.

It is in reference to certain differences in various cork-winged growths that the following study has been made, the author believing herself to have noticed some facts which may have a bearing on certain physiological questions at present under consideration. Although the number of species examined was quite limited, yet, for the sake of convenience, they may be considered as represented by three types, *Quercus macrocarpa* Michx., *Liquidambar styraciflua* L., and *Euonymus alata*. The latter genus is extremely interesting from a systematic standpoint. No two species examined agreed in the manner of cork development, while a variety differed from its species only by a slight and unimportant variation. Quercus macrocarpa, and those agreeing with it in structure, deviate less than the others from the so-called rough-barked trees, or those whose trunks are ridged and furrowed while their branches are smooth. The younger branches of Q. macrocarpa, however, are completely covered with a set of wings, generally five in number. The manner of their origin is as follows:

Anatomy of the superficial periderm of Q. microcarpa.

Stems were examined July 10, which were taken from a tree a few days before from the Arnold arboretum, and which had been kept in a fresh, growing condition. At this time the young stem was covered with a periderm of six or seven layers; even the youngest internodes on the shortest branches, some not exceeding two millimeters in length, were covered with a periderm of six or seven layers in thickness. Lenticels were very numerous over the whole internode. The wings do not originate until the internodes have reached about their full length. Their manner of origin may be said to follow a fixed law, though very many irregularities occur.

The stem, when young, is conspicuously five-angled, owing to the strongly developed leaf-traces. The periderm takes its rise from the subepidermal layer, developing uniformly around the stem till about five or six layers of cork have been formed. The epidermal cells, at first, appear to yield to this strain by stretching in the direction of the circumference until their tangential much exceeds their radial diameter. The large number of lenticels which develop at the same time with the periderm appears to diminish this strain somewhat, but as the growth of the periderm continues and the epidermal cells reach their full tension, they break at various points over the surface. At the projecting angles, where the strain is greatest, this giving way of the epidermal cells soon becomes insufficient to allow the necessary expansion, and the young, fresh periderm breaks in lines along these angles. A cross section at this stage shows from five to seven layers of periderm cells, which are living and active, as shown by the action of sugar solution when applied to them, plasmolysis at once taking place. Glycerine was tried, but produced no effect. It is quite probable it was not sufficiently dilute, as the solution was made at random in both cases. There can be no question about the result when the sugar solution was applied, and in several instances the cell nucleus was clearly seen. The tearing of these cells along the angles extends inward nearly to the phellogen layer, and, as a result, an abnormal vitality seems to be imparted to the phellogen cells immediately under the fissure. For a time this increased vitality of the phellogen layer does not extend entirely around the circumference, but only for a short distance each way from the fissure. This will be better understood by referring to the figures,* of which the first six represent this process of wing-development diagrammatically. In figure 1 the tearing of the tissue along the lines of the five angles is represented as lying at the points *a. a.* The bands of tissue represented as lying between the angles *o. o.* are composed of the original periderm of six or seven

*The plates will be published with the remainder of the text in the succeeding numbers.—EDS.

layers which first encircled the stem. In figure 2 the new growth of cells shown at *x. x.* is the product of the increased vitality of the phellogen cells near the fissure. This rapidity of growth and ability to form new cells by forming cross-walls in various directions is not confined to the phellogen layer of this vicinity, but extends also, for a limited time, to the cells produced by this layer. This is shown in figure 7 at *m.* This figure gives the actual appearance of a cross-section of stem, as represented by figure 2. Here it is evident that some of the cells, resulting from the division of phellogen cells, are themselves in the process of division. As represented in figure 2, this development of new cells extends only to the points *b. b.*, and is most rapid immediately under the line of the fissure. As growth continues for some time in about this ratio, the result is, the five sections of original periderm, *o. o.*, are not only pushed out, but the ends of each are curled toward each other, thus making a hollow furrow along the internode. This condition in its formative stages is represented in figures 4, 5 and 6, sections *o. o.*, the figures being made smaller merely for convenience as the real size of the wings increases. On testing these specimens with reagents, it was found that the cell walls of the sections *o. o.* consisted principally of suberin, while those formed later, represented by sections *x. x.*, are not true cork cells, but ligneous, and correspond to the phelloid of Höhnel. Figure 8 shows the actual appearance of these cork and phelloid cells, as represented in figure 4. Figure 9 shows merely the tip of the wing of figure 6.

This matter of difference in the chemical nature of the cell walls will be referred to again in connection with the physiology of the wings, where its consideration more properly belongs.

Returning now to the stage of growth represented in figures 2 and 3, it will be plain there are five longitudinal bands of rapidly growing tissue extending along the internode across each angle, while there are also bands between these, in which growth is for the time suspended. At what time the phellogen cells of these bands begin their activity again it is impossible to say. Sections cut from a two years old stem, of which figure 8 is an exact representation, so far as the outline of the different tissues is concerned, show that in this case growth of the phellogen cells of these five bands was suspended till toward the close of the summer's growth; then activity commenced all around the circumference of the stem, and the narrow plate cells, *y*, were formed, extending entirely around the stem. In most cases, however, it is probable that growth of the entire phellogen layer is resumed earlier in the season than in the case of the section from which figure 8 was taken, and that, for some time, the same kind of tissue is produced as that forming the first five bands, viz: phelloid tissue, referred to on the figures by *x*. After some time the fall growth occurs and the ring of plate cells, *y*, is formed. This must have been the case in figure 9, which is also an exact representation of a section from another stem. Nearly all completed wings examined agree with figure 9 in this respect. It happened that the specimen from which figure 8 was drawn was the only one found which illustrates this stage of growth, that is, the gradual throwing outward the ends of the sections *o*, *o*, which process forms the furrow. This is, therefore, given to prove the manner of growth in this respect, while it is probable that figure 9 shows the most common form in respect to the time when the whole phellogen layer resumes its activity. However this may be, it never fails that in the autumn, just before growth of the entire tree is suspended, several layers of narrow plate cells are formed, whose chemical nature is the same as that of the first periderm sections *o*, *o*. The fissure, at this time, extends in some cases entirely down to this mantle of thicker walled cells; in the specimen sketched, figure 8, still several layers are left intact between the ring of plate-cells and the outside air. In this condition the winter is passed. In the spring the entire phellogen layer resumes its activity, rapidly developing phelloid cells with thin walls and long radial diameter. This continues till the strain is too great to be borne by the walls of the surrounding plate-cells, and they break regularly along the lines of the preceding years' fissures, *a*, *a*. Growth continues during the summer nearly uniformly as the foundations for the wings are laid, and the breaking of the new tissue follows the lines already begun. At the close of the second season the same process occurs as in the preceding fall, viz.: several layers of narrow plate-cells are formed around the entire circumference. In this way large cork wings are formed, enlarging each year at the base as the stem increases in thickness. It is seldom that they are perfectly regular in their whole length, but on nearly all the older branches the number five may be recognized, and the little hollow furrow running along the top of each wing may be plainly seen. Fig. 10 shows a cross-section of a stem four years old, in which only two of the wings show the furrow, owing to the fact that at the point where this section was cut, the furrows of the remaining three wings were not perfectly developed. As the phelloderm plays no important part in the formation of cork from the standpoint of our subject, no attention was given to this throughout the study made.

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Characteristic vegetation of the North American desert.

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The term desert has a somewhat wide application. In one sense it is applied to a tract of country practically destitute of vegetation from sterility of soil. Such sterility, however, is not always the fault of the soil, but is due to the absence of water in sufficient quantity to promote vegetation. Our ideas of a desert are largely drawn from popular descriptions of some portions of the Great Sahara, where low plains covered with drifting sand, interspersed with vast fields of naked rock, spread over regions over which the traveler might pass for days without meeting with a drop of water or a blade of grass. Such cases are met with, but then occasionally an oasis is met an island of verdure, where, around cool springs of water, flourishes a tropical vegetation of palms, ferns and acacias. But this description covers only a part of what is known as the Sahara Desert.

Explorations of travelers and scientists show that the great desert is a region of elevated plains rising up into mountains of 300 to 500 feet in height, and separated from each other by valleys, immense sandy tracts at a general elevation of from 1,200 to 1,500 feet, but sinking at times into depressions which sometimes descend below the level of the sea.

The moisture from the Mediterranean Sea is arrested in its southward passage by the range of mountains running nearly parallel with it, and is mainly precipitated on the north or Mediterranean side; thus the southern slopes are left in an arid condition, the aridity increasing as the country recedes from the mountain ranges and peaks, where snow falls in the winter, and, melting in the summer, runs down the narrow courses and ravines until it is finally wasted in